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Effects of Warming on Aquatic Snails and Periphyton in Freshwater Ecosystems with and without Predation by Common Carp

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Abstract: Freshwater gastropods play key roles in shallow aquatic ecosystems, with a central position in the periphyton–gastropod–fish trophic pathway, as they feed on periphyton and are preyed on by animals of higher trophic levels. Thus, it is of great interest to explore how climate change impacts the gastropod community and the trophic cascading effects on periphyton. Here, we constructed a simplified, shallow lake food web in 24 large mesocosm tanks to simulate warming (+4.5 °C) on the population responses of two common snails (*Bellamya aeruginosa* and *Radix swinhoei*) in two different systems (without/with common carp *Cyprinus carpio*) over 200 days. We found that warming lowered the biomass and density of *R. swinhoei* by 16.8% and 41.6%, respectively, and accelerated the average time of density peak of *R. swinhoei* by 21.5 days in the common carp-absent system. The density of *B. aeruginosa* in the warming with common carp group was lowered by 79.8% more than in the warming group without common carp. The averaged biomass and density of *R. swinhoei* in the fish-present system significantly lowered by 64.4% and 92.5%, respectively, compared to the fish-absent system. Cascading effects were also observed, as the snail communities declined under warming, that is, the grazing pressure on periphyton was less, resulting in its higher biomass. In conclusion, in the fish-absent system, warming decreased the biomass and density of the *R. swinhoei*, and in both snail populations, the biomass and density were much higher than those in the fish-present system. Due to the different phenology of snail species and species-specific predation, future stronger predation in a continuous warming condition might undermine the diversity of the gastropods, thereby changing food web structures in shallow freshwater ecosystems.

Keywords: aquatic gastropod; climate change; phenological mismatch; predator; trophic cascading; timing

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1. Introduction

Freshwater gastropods can be found in nearly all aquatic habitats, where they play key roles in shallow freshwater systems [1,2]. They feed on detritus, periphyton, and even phytoplankton and macrophytes, and are, in turn, preyed on by fish and other animals, thus significantly contributing to nutrient cycling, energy transfer and the structure of aquatic food webs [3,4]. Through mixing surface sediments, breaking down organic detritus and feeding on periphyton, snails can enhance the microbial growth and alter the composition of primary producers [5,6]. Branchiate snails can increase water clarity and reduce nutrients in the water by filtering phytoplankton [4,7], and other snails can decrease shading through grazing periphyton, thus indirectly enhancing the growth of submerged macrophytes [8–12]. In addition, freshwater snails are often used for biomonitoring and assessment of metal pollution [13–15]. As one of the most diverse groups of freshwater animals, freshwater snails contribute substantially to the biodiversity of macroinvertebrates [16,17]. The composition of freshwater gastropods is also related to public health, as they are intermediate hosts of many trematode parasites [18]. However, because our planet has been experiencing unprecedented changes due to anthropogenic activities [19], freshwater gastropods are considered to be highly threatened around the world [1,17].

Fish–snail–periphyton interactions comprise a common benthic trophic pathway in aquatic ecosystems where snails are present [20,21], and benthic pathways can contribute substantially to aquatic food webs in shallow ecosystems [22]. Previous studies showed that in the absence of molluscivorous or benthivorous fish, snail biomass increased, reducing periphyton biomass [11,23]. This suggests that fish predation can significantly affect the abundance of aquatic snails, whose effects can vary significantly among prey species [24,25]. As different species might show differential vulnerability to predators [26], how predation affects snail populations by top-down control remains a knowledge gap.

Previous studies have demonstrated that warming will alter species phenology [27], distribution patterns [28], species interactions [29,30] and food web structure [31]. Habitat temperature plays a key role in regulating the metabolic rates of individuals, and species usually have limited thermal tolerance [32,33]. Warming can affect the timing of reproduction and the fecundity of invertebrates [34,35]. Warming might induce shrinking body size of snails, as small-sized specimens are more efficient at meeting the higher metabolic demands in a warming environment [36–38]. Moreover, warming could increase the strength of consumer–resource interactions, such as the top-down control of snails on periphyton [30,39]. However, warming will also elevate the metabolic demands of predators, which might strengthen the predator–prey interactions [40,41], and warming can enhance the competition between ectothermic herbivores that share the same resources by phenological mismatch and basal resources [42]. To our knowledge, there has been little published about the snail community response in a warming environment with the absence or presence of a predator.

Here, we conducted a mesocosm study to explore the response of two common freshwater snail species and periphyton to warming in two different systems (without/with fish). We tested the predictions that (1) warming in a fish-absent system alters the phenology and decreases the abundance of snails through enhancing competition, and increases the biomass of periphyton; (2) fish presence alone reduces the abundance of snails due to selective feeding and increases the biomass of periphyton; (3) warming in a fish-present system enhances the top-down control of fish predators on snails and increase the biomass of periphyton.

2. Materials and Methods

2.1. Study Species

The targeted two gastropod species, *Bellamya aeruginosa* and *Radix swinhoei*, are widespread in China, and they commonly coexist in shallow aquatic ecosystems [43]. *B. aeruginosa* is a branchiate gastropod consumed by humans [44,45], which feeds on sediment organic detritus, algae and bacteria [46], providing food for common carp [47]. The species is gonochoristic and ovoviviparous and has a minimum reproductive temperature of 16 to 18 °C, but optimally about 26 °C [48]. Adult females gestate throughout the year, breeding for about 6 months and releasing offspring continuously, each producing about 50 offspring per year [45].

R. swinhoei is a common pulmonated gastropod, which mostly lives among macrophytes and feeds on detritus, macrophytes, algae and dead animals [49,50]. It is hermaphrodite and allogamous, and it can breed multiple times a year [49]. Members of its genus are generally cold-adapted gastropods [51], including *R. balthica*, which prefer an optimum temperature of 16–20 °C and fail to reproduce over 24 °C [52,53], living on average 30 weeks [54].

2.2. Experiment Set-Up

A total of 24 insulated, cylindrical, polyethylene mesocosms (each 2500 L in volume, 1.5 m diameter, 1.4 m high) were placed outdoors at Huazhong Agricultural University, Wuhan, China, and were used to simulate shallow lake ecosystems. Top layer sediment was collected from Lake Liangzi (N 30°11′3″, E 114°37′59″), which is a mesotrophic lake, with TN and TP in the water column there averaging 0.43 mg L^{-1} and 0.023 mg L^{-1}, respectively. The location is rich in macrophytes, including *Potamogeton crispus*, *Hydrilla verticillata*, *Ceratophyllum demersum* and *Trapa* sp. All mesocosms were filled with 10 cm of homogenized sediment on the bottom, and tap water was filled to 1 m depth. Both snail species were recovered from the collected sediment, and no differences in the initial biomass (10.19 ± 4.55 g/m^2) and density (6.49 ± 1.75 ind/m^2) were found for the snails in the different treatments. The experiment ran from February 2, 2015, to November 18, 2015, with the first month being acclimation without treatments.

There were two treatments without fish, one at environmental temperature (C) and one at increased (+4.5 °C) temperature (W), and two treatments where fish (one 60 g common carp *Cyprinus carpio*, length about 15 cm, age < 1 year) were added [55], one at environmental temperature (F) and one at increased (+4.5 °C) temperature (WF) [56]. The temperature increase of +4.5 °C was chosen to simulate the possible warming that could happen in this region at the end of this century [57], and the temperature was manipulated automatically using two temperature sensors and a heating element controlled by a computer [58]. Common carps are a common omnivorous species that coexist with the two snails in water bodies in China, and the biomass of the carps in the mesocosms (equal to 340 kg ha^{-1}) was within the range found in the lakes of this region [55,59]. Carps of this size consume these juvenile snails. All carps were commercially obtained from a local aquarium shop. Carps were temporarily raised in an environment without food for 24 h prior to the experiment. There were 6 replicates for each treatment, and all 4 treatments were randomly assigned to 24 mesocosms.

To indicate how the treatments affect the water quality during the experiment, water samples were collected once a week to analyze total nitrogen (TN), total phosphorus (TP), chlorophyll a (Chl-a) and turbidity. TN and TP were first digested by alkaline potassium persulfate in an autoclave (120 °C, 1.1 kg cm^{-2}) for 30 min. TN was analyzed by UV spectrophotometry (UV-2800, Unico, China, GB 11894-89) and TP with the ammonium molybdate spectrophotometric method (GB 11893-89). Chl-a was determined by filtering water in Whatman GF/C filters, and spectrophotometric analysis was performed after acetone extraction (HJ 897-2017). Turbidity was measured with a portable WGZ-2B turbidity meter (Xinrui, Shanghai, China). Periphyton Chl-a was measured by attaching an unglazed ceramic tile (10 * 10 cm^2) vertically to the middle of each mesocosm wall. It was removed weekly, and the algae were brushed off and extracted in acetone solution for 24 h, then analyzed by spectrophotometry. The biomass of the periphyton was expressed as the concentration of Chl-a per square meter area.

The density and biomass of snails were monitored once a week from 14 March 2015, to 25 October 2015. Snails were collected by vertically placing a tube (1.5 m in height, 4.5 cm in outside diameter, a total surface area of 0.1413 m^2) attached to the wall of the mesocosm, and the bottom of the tube was inserted into the sediment. The tube was removed once a week, and all snails were collected, blotted dry, counted and weighted to 0.0001 g, and then released back into the mesocosms.

2.3. Analyses

All statistics were performed in R version 4.1.2 [60]. To analyze the effects of warming on snail biomass, water quality, Chl-a and periphyton concentrations in the two systems (without fish and with fish), multiple linear mixed-effects models (LME) were used, with the sampling date and mesocosm ID as random factors. These dependent variables were log-transformed to increase the normality of the distribution. The normality and homoscedasticity of the dependent variables were assessed visually by plotting model residuals versus fitted values in quantile-quantile plots of the model residuals. As the densities of both snails were count data, a Poisson link function was applied to the generalized linear mixed-effects model (GLMM). The analysis of variance parameters for the fixed factors of the mixed-effects models were then calculated using Type II Wald χ^2 tests. All linear mixed models were performed using the lme4 package [61]. Differences among the four treatments were compared using the emmeans package after the linear model test.

To assess the distribution patterns of the biomass and density of the snails over time, data from each mesocosm were fitted with six parameters of the Weibull function using the candidates package, which is designed for peak curve fitting. Not all peak curve fittings were trustable. Only the results of the biomass and density of *R. swinhoei*, as well as some of the *B. aeruginosa* in the control (C) and warming treatments (W) without fish present, had good fit, as the rest did not correspond to any trends (Table S2). The heights and timing of peaks between the control (C) and warming treatments (W) for *R. swinhoei* were compared using independent t-tests. Normality and homogeneity of variance were checked using a Shapiro test and an *F*-test, respectively. To evaluate possible differences between the two snail species in all treatments, normalized data (data were divided by the maximum value of each snail in each mesocosm to diminish their different scales) from the two species were plotted together.

To evaluate the possible effects of warming with fish present on the respective biomass of the two snail species and periphyton directly and indirectly, a mixed-effects structural equation model was constructed using lme4 and the piecewiseSEM package, with sampling date and mesocosm ID as random factors. In the model, warming and fish were categorical external predictors, and snails and periphyton biomasses were continuous response variables. The final model with the lowest Akaike Information Criterion (AIC) value included only significant paths, and we assessed model fit using Fisher's C [62].

3. Results

3.1. Treatment Manipulation

Daily mean temperature was 4.25 ± 0.42 (n = 223, total number of days, mean ± sd) higher in the warmed mesocosms (Figure 1a). In the treatments without fish, warming (W) significantly increased Chl-a concentration in periphyton samples (Tables 1 and S1). In the treatments with fish, warming (WF) significantly increased turbidity and Chl-a concentration in periphyton samples (Table 1 and Figure 1b,d). Adding a carp predator to mesocosm tanks system (F) significantly increased turbidity and concentrations of Chl-a in the water column and periphyton, compared to the control (C) group (Figure 1b–d). Data for TN and TP can be found in Figure S1. There was no significant change in carp biomass at the end of the experiment for any treatment.

Table 1. Effects of warming on the measured response variables and snail biomass and density in two systems (without/with fish). Water turbidity, Chl-a concentration of the water column and periphyton, and snail biomass were analyzed using linear mixed-effects models, and snail densities were analyzed with generalized linear mixed-effects models and a Poisson link function. Bold number indicates significance < 0.05.

		Without Fish		**With Fish**	
	Parameters	**F/χ^2**	***p***	**F/χ^2**	***p***
Measured response variables	Log (Turbidity + 1)	0.195	0.668	13.119	**0.005**
	Log (Chl a + 1)	1.289	0.283	4.840	0.053
	Log (Periphyton + 1)	27.593	**<0.001**	14.597	**0.003**
B. aeruginosa	Log (Biomass + 0.01)	2.029	0.185	3.725	0.082
	Density	2.007	0.157	3.692	0.054
R. swinhoei	Log (Biomass + 0.01)	5.910	**0.035**	0.112	0.745
	Density	4.269	**0.039**	0.201	0.654

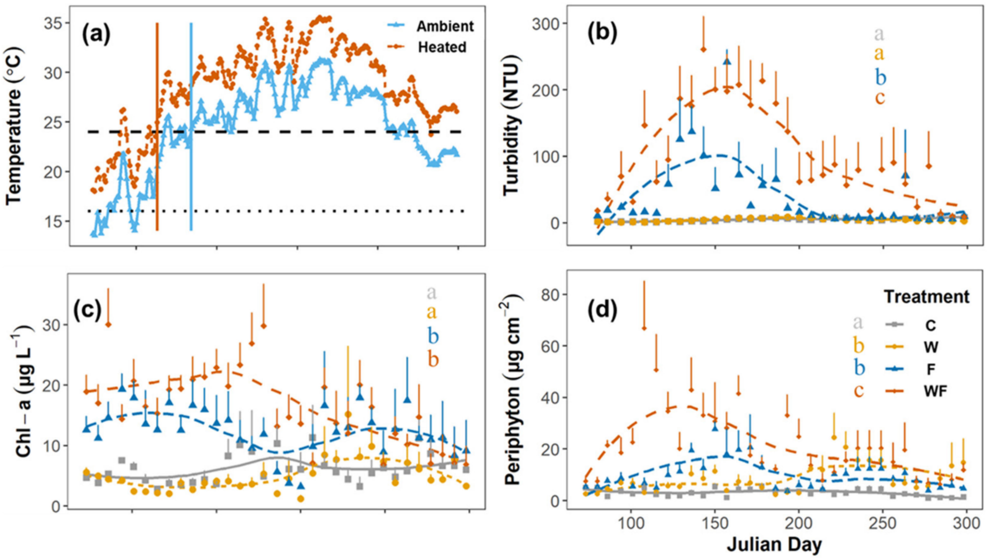

Figure 1. Daily average temperature (**a**), water turbidity (**b**), and Chl-a concentration in the water column (**c**) and periphyton (**d**) changed over time in different treatments. In panel (**a**), the horizontal dotted and dashed lines indicate temperatures of 16 °C and 24 °C, respectively. When the average temperature started to go above 24 °C, the days were 113 and 134 for the warming and ambient treatments, and these are indicated by vertical red and blue lines, respectively. The curves were fitted from the LOESS model in R package ggplot2. Panels (**b**–**d**) share the same legend. Vertical bars are standard errors. Small letters indicate significant difference between the four treatments. C for control, W for warming without fish, F for fish present alone and WF for warming with fish.

3.2. Snail Species Responses

In all treatments, snail biomass was dominated by *B. aeruginosa* (89.01% on average). Snail density was dominated by *R. swinhoei* (82.16% on average), but only when without carp (C and W) (Table S1, Figure 2). In both different systems (without and with fish), the biomass and the density of *B. aeruginosa* did no differ between temperatures (C and W, F and WF separately), but warming with fish (WF) significantly reduced the biomass (26.7%) and density (84.9%) of *B. aeruginosa*, compared to the control (C) group, and significantly reduced the density (79.8%) of *B. aeruginosa*, compared to the warming without fish (W) treatments (Tables 1 and S1 and Figure 2a,b). In the fish-absent system (C and W), warming (W) resulted in a significantly lower biomass and density of *R. swinhoei* by 16.8% and 41.6%, respectively (Table S1). The biomass and density of *R. swinhoei* did not differ between warming with fish (WF) treatments and fish alone (F) treatments, and the average biomass and density of *R. swinhoei* in the fish-present system (F and WF) significantly lowered by 64.4% and 92.5%, compared to the fish-absent system (C and W) (Tables 1 and S1 and Figure 2c,d).

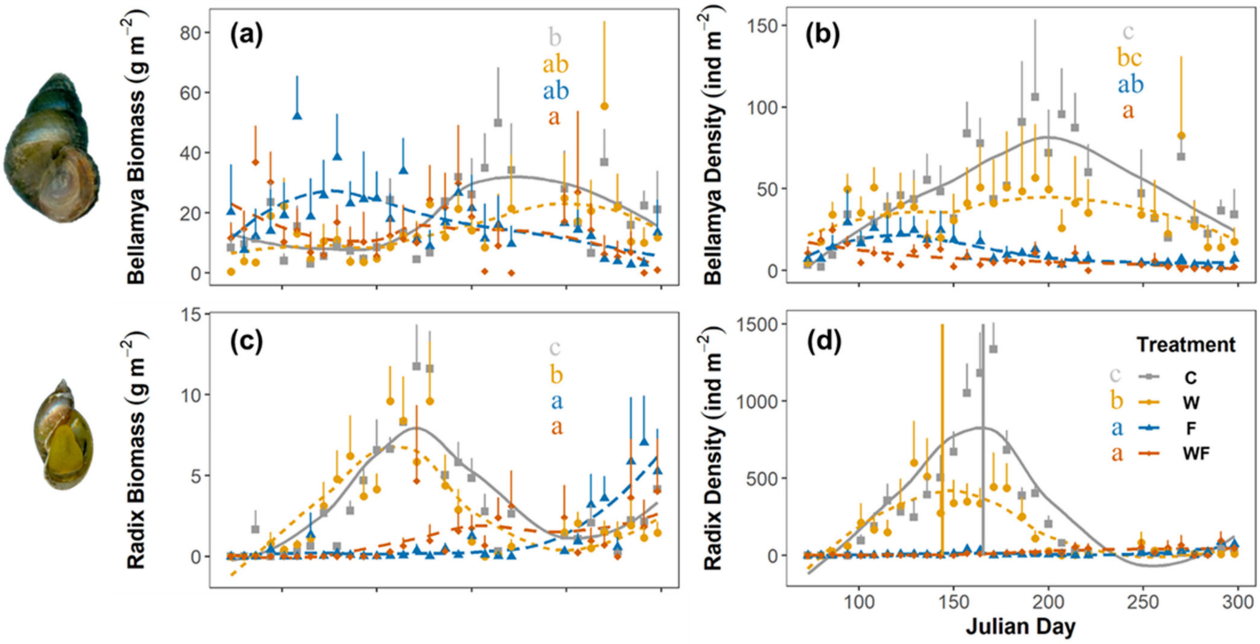

Figure 2. Biomass and density of populations of the two snail species changed over time in different treatments. Biomass (**a**) and density (**b**) of *B. aeruginosa*, and biomass (**c**) and density (**d**) of *R. swinhoei*. The curves were fitted from the LOESS model in R package ggplot2. Vertical bars are standard errors. The vertical lines in panel (**d**) indicate the time of the peak density extracted from the fitted Weibull functions, and the time of peak density for the warming with fish (W) treatment was 21 days earlier than the control (C). The curves were fitted using the LOESS model in the R package ggplot2. Small letters indicate significant difference between the four treatments. C for control, W for warming without fish, F for fish present alone and WF for warming with fish. Please note that the *y*-axis has a different scale for each species.

The average time of peak density in the *R. swinhoei* population occurred 21.5 days earlier in the warming without fish treatment (W) than in the control (C) treatment (Welch *t*-test, Table S3). However, the peak densities, peak biomass, and average time to the latter of *R. swinhoei* did not differ significantly between the warming without fish treatment (W) and the control treatment (Table S3). The timing of peak biomass and density for *B. aeruginosa* varied widely within treatments, with variations increased in the warmer conditions (without fish), compared to the control ambient conditions, with some occurring faster ($n = 4$) and one slower ($n = 1$) (Table S2 and Figure S2). No clear peak for the two snail species occurred in the treatments with carp.

3.3. Structural Equation Model

The structural equation model confirms that warming (standardized path coefficient, SPC = −0.20) and carp presence (SPC = −0.24) negatively affected the biomass of *B. aeruginosa* (overall explanation $r^2 = 0.18$, Figure 3). Only carp presence significantly reduced the biomass of *R. swinhoei* (SPC = −0.49, $r^2 = 0.43$). Warming (SPC = 0.31) and carp presence (SPC = 0.41) both increased the biomass of periphyton ($r^2 = 0.48$), which was suppressed by *R. swinhoei* (SPC = −0.13).

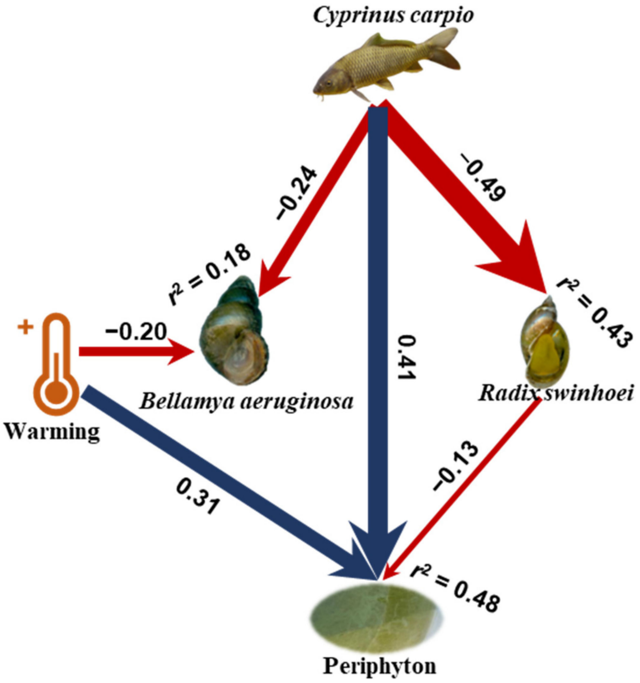

Figure 3. Structural equation model showing the effects of warming with carp (*Cyprinus carpio*) presence on biomass of the two snails (*B. aeruginosa* and *R. swinhoei*) and periphyton. The goodness-of-fit test of the model is Fisher's C = 8.615, $p = 0.196$, df = 6. Exogenous variables are indicated by rounded rectangles, and endogenous variables are represented by ovals. Coefficients of determination (r^2) are shown for all endogenous variables. Numbers adjacent to arrows are standardized path coefficients and indicative of the effect of the relationship. Positive and negative effects among variables are depicted by blue and red arrows, respectively, with arrow thicknesses proportional to the strength of the relationship. All relationships in the model are significant at $p < 0.05$.

4. Discussion

4.1. Warming (without Fish) Effects on Snails

In our study, warming (W) significantly advanced the reproduction peak of *R. swinhoei* by 21.5 days. Prior studies have shown that warming advances the phenology of species across different trophic levels, including plants, algae, zooplankton [63] and fish [64], with the phenology of primary consumers generally advanced more than other trophic levels [27]. In our study, the number of earlier reproduction days of *R. swinhoei* under the warming treatment (W) matched the number of days when the temperature reached >24 °C in advance. Species in the genus (*Radix*) are normally cold-adapted [51]; therefore, when temperatures reached >24 °C, the snails did not reproduce [52,53]. In contrast, no consistent peaks of biomass and density were detected for *B. aeruginosa*, which might be due to their different life-history traits. *B. aeruginosa* has a much higher upper-limited thermal tolerance, as its optimal reproduction temperature is ~26 °C, and the female can remain gravid all year round and release offspring continuously [45]. Field investigations have also found multiple different peaks of abundance and biomass for *B. aeruginosa* throughout the year [65–67]. However, the time of peak biomass and density of *B. aeruginosa* in our mesocosms showed differences between the ambient (C) and warming treatment (W) in the absence of fish, which indicates that warming could alter the phenology of the snail; most warming treatments showed advanced phenology, but several treatments showed delayed phenology (Table S2 and Figure S2). This might indicate that the effects of warming on the snail were different among different-aged individuals, which needs to be further explored.

Warming (W) lowered the overall biomass and density of *R. swinhoei*, but did not cause differences in *B. aeruginosa* biomass and density, which may be linked to their phenology and feeding rates. *R. swinhoei* is cold-adapted and its reproductive cycle can be completed in 8 weeks, whereas *B. aeruginosa* has a much higher thermal tolerance and its reproductive cycle extends for about 6 months [45]. Thus, *B. aeruginosa* would respond slower to rising temperatures from spring to summer, whereas *R. swinhoei* would stop reproduction, and their survival rate would decline as the temperature exceeds 24 °C. However, in the warming (W) treatments, the faster response of *R. swinhoei* reproduction could expand the population faster and then enhance competitiveness, which may suppress the *B. aeruginosa* population, as clear decreases were observed in the biomass and density of *B. aeruginosa* when these peaks reached for *R. swinhoei* in the warming treatment (Figure S3). This might be because *R. swinhoei* depleted algal food resources in the growing season (Figure 3). In our study, the standing biomasses of periphyton were low in both the ambient (C) and warming (W) treatment in the early growing season. These indicate a strong grazing pressure of the snails on periphyton during this period. Furthermore, the periphyton abundance did not increase at the same rate as the snail populations under warming [27]. Therefore, there were fewer resources available when the snails reproduced in the warmer conditions, and *R. swinhoei* may be more competitive in the reproductive season.

4.2. Warming (with Fish) Effects on Snails

There was no direct effect of warming on the biomass and density of the two snail species in the common carp presence system. Here, the common carp exerted stronger pressure on *R. swinhoei*, the preferred food, irrespective of warming. The reason could be that fish predation in our mesocosms was too strong (reduced the density of *R. swinhoei* by 92.5%), thus overriding a possible warming effect. Warming has been shown to affect attack rate, handling time and predation success [68]. However, in our study, the prey is a slow-moving species, the impact of warming on predation was mainly determined by the increased feeding rate of the carp, and the prey is unlikely to develop avoidance mechanisms against predation in one or two generations. In a longer period, continuous warming and strong predation might eventually affect the coexistence of the two snail species to exclude *R. swinhoei*.

4.3. Predation Effects on Snails

As expected, the biomass and density of the two snails were lower in the fish-present system than that in the fish-absent system [24,25]. The predation effects were particularly strong on *R. swinhoei* and the juveniles of *B. aeruginosa*. This is because common carp can only prey on snails smaller than their jaw gape; hence, they substantially eliminated the juveniles of both snails. Moreover, the carp also may directly prey upon the eggs of *R. swinhoei*, as shown for eggs of white sturgeon [69]. Furthermore, the biomass of the adult individuals was greater in *B. aeruginosa* (which can reach 5.77 g) than in *R. swinhoei* (1.5 g or less), and shell toughness is much greater in *B. aeruginosa* than in *Radix* spp. snails [47,70], making the former more difficult to consume. Thus, adult *B. aeruginosa* dominated in the predation treatment (Figure S4), particularly in the beginning, because *R. swinhoei* were preferentially consumed by the fish. This suggests that predation increased the relative abundance of *B. aeruginosa* over *R. swinhoei* at the early time, and the competence shifted over time. Under stronger predation pressure, *B. aeruginosa* might exclude *R. swinhoei* by altering the balance between the possibly competing species [71,72].

5. Conclusions

In the fish-absent system, warming decreased the biomass and density of the *R. swinhoei*, and both snail populations' biomass and density were much higher than in the fish-present system. Warming resulted in higher periphyton biomass in both the fish-present and fish-absent groups (Figure 3). The trophic cascading effects could have a substantial impact on aquatic food webs. With the decrease of gastropods, the fish population might decrease over time [73], but periphyton growth could increase, resulting in a bottom-heavy trophic pyramid. This might hinder the nutrient cycle and energy transfer in the aquatic ecosystem [74]. Furthermore, stronger predation in continuous warming conditions might undermine the coexistence of the two snails, eventually causing the local extinction of the less dominate species. The loss of key primary consumers might weaken the stability of aquatic food webs and decrease biodiversity [75,76]. In addition to warming, shallow lakes face anthropogenic problems, such as eutrophication, chemical pollution and habitat destruction [19,77]. These might interactively alter the shallow aquatic ecosystem from a healthy state to a nuisance state (dominated by phytoplankton or benthic algae), leading to a loss of ecosystem functions and services [78,79].

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/w15010153/s1, Figure S1: Concentrations of TN and TP in the water column changed over time; Figure S2: Biomass and density of the two snails changed over time in each mesocosm of control and warming treatment without fish present; Figure S3: Relative biomass and density of both snails in each treatment; Figure S4: Mean size of the snails during the experiment in each treatment; Table S1: Means of the measured response variables and snail biomass and density during the experiment for different treatments; Table S2: Weibull fitted results for biomass and density of each snail in each mesocosm in the control and warming treatment without fish; Table S3: Differences of peaks of biomass and density of *R. swinhoei* between control and warming treatment without fish present.

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Informed Consent Statement: Not applicable.

Data Availability Statement: The datasets used during the current study are available from the corresponding author on reasonable request.

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Conflicts of Interest: The authors declare no conflict of interest.

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